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Reproductive Biology of Pigs

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Lloyd L. Anderson, distinguished professor of animal science

Summary and Implications

This report describes aspects of sexual development and maturation, hormonal regulation in boars, hormones and puberty in gilts (including the environment and hormone treatment, estrous cycle, ovulation rate, conception rates, embryo survival, and litter size), pregnancy, lactation, and sows at weaning. In addition, genes that affect these developmental and reproductive processes are included.

Sexual Development and Maturation

Genetic sex determines the development of gonadal sex, which in turn determines phenotypic and reproductive characteristics. The Y chromosome and genes located on autosomes are critical to the development of gonads (testes or ovaries) which are eventually capable of gametogenesis (spermatogenesis or oogenesis). The sex-determining region Y (*SRY*) gene is located on the Y chromosome and initiates development of testes rather than ovaries from early biopotential gonads. It triggers differentiation of Sertoli cells from supporting cell precursors, which would otherwise yield follicle cells. A related autosomal gene, *Sox9*, is essential for Sertoli cell differentiation. The *SRY* gene has been assigned to the distal portion (p12-p13) of the short arm of the Y chromosome in pig and encodes testis determining factor (*TDF*). The *TDF* is necessary for development of the male reproductive system, phenotypic sex, and typical male behavioral characteristics. The porcine embryo has 19 pairs ($2n=38$) of chromosomes.

In eutherian mammals, sex determination is equivalent to testis determination. In testicular organogenesis, the germ cells are attracted to and encapsulated with somatic cells, initially in arrangements as seminiferous cords, which are delineated by connective tissue. The cords of cells eventually hollow into seminiferous tubules with connections to mesonephric tubules. Somatic cells within the seminiferous tubules differentiate into sustentacular cells (supporting or Sertoli cells). Between seminiferous tubules, mesenchymal cells differentiate into interstitial cells (Leydig cells) that secrete testosterone which induces normal male phenotypic development (Table 1).

In the female conceptus, oogenesis occurs later with the obvious feature being the absence of testicular-inducing patterns of organogenesis. The ovarian cortex proliferates, and germ cells (oogonia) transform into

oocytes and enter early phases of premeiosis before they become separated from mesenchyme by a single layer of differentiating follicle (pregranulosa) cells. The primary follicles prevent oocytes from entering meiotic processes beyond the diplotene phase, and oocytes remain in this resting stage until puberty.

Mesonephric tubules stabilize in the male conceptus as the Wolffian ducts (e.g., epididymides, vas deferens, seminal vesicles, and prostate and bulbourethral [Cowpers] glands), whereas in the female conceptus, the paramesonephric tubules survive as the Müllerian ducts (e.g., oviducts, uterus, cervix, and the upper part of vagina). Both types of ducts are present in early embryonic development, giving a conceptus the capability of developing either male or female internal and external genitalia. Testes are body sex differentiators because they impose masculinity on the developing genital tract and on secondary sexual features and behavior. In their absence, or in the presence or absence of the ovaries, the genital tract and secondary sex characteristics develop as a normal female. The secretion of antiMüllerian hormone (AMH, or Müllerian-inhibiting substance [MIS]) by the testes induces regression of the Müllerian ducts. Mapping on porcine chromosomes has identified seven genes that implicate this developmental pathway. Four genes were mapped: *AMH* and *WT1* (Wilms' Tumor gene 1) on chromosome 2 (SSC2), and placental *CYP19* (cytochrome P450) and *FTZFI* (fushi tarazu factor 1, alias *SFI* [steroidogenic factor 1]) to pig chromosome 1 (SSC1). Four other genes were regionally located: a second *CYP19* gene, *AHC* (adrenal hypoplasia congenital), *SOX2* and *SOX9* (*Sry*, sex determining region Y). The normal level of *SOX9* expression in Sertoli cells depends on *SRY* and *SFI*.

Cellular and nuclear growth of germ cells increases from the oogonial stage (13 μm in diameter) to the oocyte within a primordial follicle (27 μm in diameter) and during early stages of meiotic prophase (leptotene, zygotene, and pachytene). The oocyte in the diplotene stage continues to increase in diameter during follicular maturation; growing follicles increase approximately threefold. Oocytes increase to a maximum diameter of 120 μm in Graafian follicles near the time of ovulation, and the zona pellucida consists of a homogeneous matrix approximately 8.6 μm in thickness. Surface area of the cell membrane (vitelline membrane) is increased by irregularly spaced microvilli in contact with cell processes arising from coronal radiata banding the zona pellucida. Cortical granules about 0.2 μm diameter are numerous immediately beneath the oocyte membrane wall. Other features of the oocyte cytoplasm include yolk globules and mitochondria (approximately 200,000).

Corona radiata cells are porcine granulosa cells on the outer aspect of the zona pellucida that are arranged in a radial pattern. These cells adhere to each other and project microvilli through the zona pellucida and perivitelline space

that terminate in the oocyte membrane wall. They are nurse cells for the growing oocyte during oogenesis; their nutritive material is conveyed by extensive cytoplasmic processes. These cells disappear soon after ovulation. Cortical granules are extruded through the vitelline membrane on contact with the fertilizing sperm, resulting in prevention of polyspermy.

Hormones and Puberty in Boars

Porcine blastocysts synthesize estrogens by day 12. Fetal testes contain Δ^3 - 3β -hydroxysteroid dehydrogenase (3β -HSD) about day 35 before differentiation of Leydig cells, and they secrete testosterone during differentiation of the internal and external genitalia. Differentiation of the Wolffian duct and development of the seminal vesicles, prostate, bulbourethral glands, and external genitalia occurs between days 26 and 50.

Serum testosterone concentrations are low during the later half of fetal development. Testosterone production late in fetal life becomes gonadotropin dependent. Circulating luteinizing hormone (LH), follicle stimulating hormone (FSH), and prolactin reach peak levels during the first week after birth, and then gradually decrease by the seventh week. Elongation of seminiferous tubules increases at this time by FSH stimulation of Sertoli cells.

Testicular Morphology

Testicular descent begins about day 60 of fetal life with growth of the gubernaculum. Testes traverse the inguinal canal (*vaginal process*) about day 85 and move to the base of the scrotum soon after birth. LH and testosterone blood concentrations parallel testicular development during these prenatal and postnatal periods.

From 40 to 250 days of age, the weight of the paired testes increases markedly from 6 to 120 grams. Circulating testosterone concentrations increase as pubertal development progresses and then decline near maturity. Estradiol- 17β serum levels increase steadily throughout pubertal development. Dehydroepiandrosterone sulfate and the 16-androstenes act as precursors to androgenic hormones in the boar. Estradiol- 17β plays a synergistic role with testosterone in sexual behavior and stimulates accessory sex glands as well as enhances testicular synthesis of testosterone.

Sexual Behavior

Mounting activity occurs early (erection by 4 months), but sequential patterns of sexual behavior culminate after 5 months. First ejaculates occur at 5 to 8 months of age; heritability (h^2) estimates for age at puberty average 0.32. The number of spermatozoa and semen volume continue to increase during the first 18 months of life. The duration of the spermatogenic cycle (spermatogonia to mature spermatozoa) is approximately 34.4 days. The duration for transit of the spermatozoa through the epididymis is about 10.2 days. Testosterone

sustains secretory activities of the accessory glands (e.g., seminal vesicles, prostate, bulbourethral glands), and these seminal fluids constitute a large proportion of the total ejaculate in the boar.

Hormones and Puberty in Gilts

Fetal gonad differentiates to an ovary at about day 35 by the appearance of egg nests (Table 1). Primary and secondary follicles appear late in gestation. FSH-secreting cells are identified in fetuses 70 days old, and serum levels of FSH, LH, and prolactin increase preceding birth.

Gonadotropin-releasing hormone (GnRH) is secreted from hypothalamic neurons and is transported through hypophyseal portal veins to the anterior pituitary where it stimulates synthesis and secretion of LH and FSH, hormones essential for normal gonadal development and function. Increased excitatory signals and reduced inhibitory signals to the GnRH neuronal network prompt the onset of puberty. Kisspeptins are potent stimulators of the gonadotropic axis. Structurally related peptides, kisspeptins, are products of the KISS1 gene. In prepubertal gilts either central or peripheral infusion of kisspeptin increased serum concentrations of LH, but not FSH or growth hormone (GH), and played a role in the mechanism involved in initiating puberty. Gilts which have a high growth rate (>700 g/day) can be inseminated between 185 and 209 days of age because the farrowing rate, culling rate and total born produced over three parities are not impaired when compared with gilts mated at >210 days. The minimum weight at mating was 127 kg. In a 2,400-sow herd, Landrace \times Yorkshire gilts expressed first standing estrus at 195 days of age, 106 kg bodyweight and 13.0 mm backfat. Mean litter size in the first three parities was highest in gilts that had expressed their first estrus between 181 and 200 days of age.

Ovarian Morphology

Puberty is characterized by first estrus, ovulation of Graafian follicles, and the release of ova capable of fertilization. The porcine NALP5 gene is an oocyte specific gene required for early embryonic development, gametogenesis, and folliculogenesis.

Environment

The age of puberty may be influenced by the level of nutrition, social environment, bodyweight, season of year, breed, disease or parasite infestation, and management practices. The presence of boars reduces age (191 vs. 232 days) and bodyweight (105 vs. 116 kg) to puberty. Puberty also is delayed in gilts penned individually as compared with those maintained in groups of 30 animals.

Estrous Cycle

Onset of estrus is characterized by gradual changes in behavioral patterns (e.g., restlessness, mounting of other animals, lordosis response), vulva responses (e.g., swelling, pink-red coloring), and occasionally a mucous discharge.

Sexual receptivity averages 40 to 60 hours. The pubertal estrous period usually is shorter (47 hours) than later ones (56 hours), and gilts usually have a shorter period of estrus than sows. Breed, seasonal variation (e.g., longest estrus in summer and shortest in winter) and endocrine abnormalities affect the duration of heat.

Ova are released 38 to 42 hours after the onset of estrus, and the duration of this ovulatory process requires 3.8 hours. Ovulations occur about 4 hours earlier in mated than in unmated animals. The length of the cycle is about 21 days (range of 19 to 23 days). The domesticated pig is polyestrous throughout the year; only pregnancy or endocrine dysfunction interrupts this cyclicity.

Steroid-secreting activity of corpora lutea (CL) in the ovaries is indicated by concentrations of progesterone and estrogen throughout the cycle (Fig. 1). Circulating progesterone levels are low at estrus (day 0), increase abruptly after day 2, reach peak values by days 8 to 12, and then decline precipitously thereafter to day 18. Estrogen concentrations increase coincident with the decline and disappearance of progesterone (Fig. 1). Peak values occur 2 days preceding estrus and reflect rapid growth and maturation of Graafian follicles during late proestrus. Soon after estrus, estrogen declines and remains low during the luteal phase of the cycle. Estradiol secreted by the developing preovulatory follicles stimulates the preovulatory surge of gonadotropins. Cyclic adenosine monophosphate (cAMP), proteoglycans, LH receptors, epidermal growth factor (EGF) and transforming growth factor- β (TGF- β) modulate steroidogenesis in porcine theca and granulosa cells. These growth factors produced by theca and granulosa modulate, in a paracrine or autocrine way, steroidogenesis and follicular differentiation. The lifespan and secretory function of this ephemeral structure in the pig can be prolonged by pregnancy or hysterectomy.

FSH in peripheral serum peaks on days 2 and 3 after the onset of behavioral estrus (Fig. 1). Ovarian follicles depend on secretion of adenohipophyseal gonadotropins (FSH and LH) for their growth and maturation. Ovarian follicular fluid of sows contains inhibin, a protein hormone, which suppresses FSH secretion. FSH serum levels are inversely related to inhibin during the late follicular phase; inhibin concentrations decrease with the LH surge.

LH plasma levels show one sharp peak at estrus and drop to low levels during the remainder of the cycle (Fig. 1). From days 12 to 15 of the estrous cycle an episodic pattern FSH and LH, as well as estradiol, secretion occurs; prolactin levels peak during estrus and remain low during the luteal phase of the estrous cycle. Prolactin levels peak when estrogen is highest, and during estrus prolactin profiles coincide better with the FSH peak than with the preovulatory LH peak. The hypothalamus in the lower part of the brain is required for the tonic inhibition of prolactin secretion, and for the regulation of both

episodic release and tonic inhibition of basal secretion of LH, FSH, and GH in the pig.

Ovulation Rate

Ovulation rate in pigs is one of the most important traits for reproduction because it directly influences litter size. A total of 15 quantitative trait loci (QTL) affecting ovulation rate has been observed, with most of them on chromosomes SSC8, SSC9, SSC13 and SSC15. This has been narrowed to the region at the telomeric end of the short arm on SSC8 using gene and microsatellite markers within the first 27 centi-Morgans (cM) and includes the GnRH receptor gene (*GNRHR*) that is critical in endocrine regulation of reproduction. A prolactin receptor gene (*PRLR*) was localized on SSC16 for different reproductive traits with a significantly higher ovulation rate for AA genotypes compared with BB genotypes.

The number of stillborn piglets averages 0.5 through the first 4 gestations and increases to 1.0 by the eighth gestation. Significant QTL for number of stillborn piglets were found on SSC4, SSC5 and SSC13. The POU domain class 1 transcription factor 1 (*POU1F1*) gene on SSC13 with regard to GH and prolactin serum concentrations of growing sows revealed differences among genotypes. These hormones are critical for the development of mammals and *POU1F1* could be a candidate gene concerning the number of stillborn piglets.

Conception Rate

The fertilization rate in pigs is usually high (>90%). Low or high ovulation rates have little or no effect on fertilization rates. Loss of the whole litter may result from fertilization failure or death of all the embryos. Early embryonic death results in resorption of the conceptus, whereas losses occurring after day 50 may result in abortion, fetal mummification, or delivery of stillborns at term.

Embryo Survival

At least 40% of the embryos are lost before parturition. Within the first 18 days, embryonic survival is reduced by 17%. By day 25, approximately 33% of the embryos die, and this can increase to 40% by day 50. Although sows have greater fecundity than gilts, they lose a greater proportion of their embryos during the first 40 days.

Litter Size

Reproductive performance is measured primarily by the number of living piglets at birth or by the total farrowing or weaning weight of pigs produced by the dam within 1 year. Ovulation rates continue to increase with subsequent gestations, but litter size reaches maximal levels by the fourth or fifth parity. Two primary uterine factors affecting uterine capacity are uterine blood flow and uterine protein secretion. Uterine blood flow increases throughout gestation but it appears maximal at around five fetuses per uterine horn; flow does not increase with further increases in the number of fetuses present. Primary placental factors affecting uterine

capacity are the size of the placenta and the efficiency of nutrient transport. QTL regions for litter size are located on SSC8 and SSC11. Candidate genes that influence litter size are *FSHb* on SSC2, leptin gene (*LEP*) on SSC18, and retinol-binding protein 4 (*RBP4*) on SSC14.

Pregnancy

Growth of Conceptuses

Ova are fertilized in the ampulla of the oviduct, and their arrival is aided by the rapid beat, in a downward direction, of cilia on the mucosal surface; in the isthmus of the oviduct, there is an upward ciliary current that may aid sperm ascent. Embryos are usually in the four-cell stage when they enter the uterus. Cleavage advances to morula stage by day 5 and then blastocyst formation by days 6 to 8. Hatching describes at least partial escape of the embryo from the zona pellucida, and it occurs on the sixth day when blastocysts may reach a size of 150 cells or more (Fig. 2). Blastocysts are unevenly distributed throughout both uterine horns. Rapid development of conceptuses is indicated by intrauterine migration of the embryos, spacing of the embryos, and transition of blastocysts from spherical to extremely elongated forms and subsequent embryogenesis. By day 11, half the blastocysts rapidly elongate to filamentous forms, often exceeding 60-100 cm, and by day 13, embryos have completed this process. These conceptuses become regularly spaced with no overlap of tubular membranes from other embryos in that horn.

Normal embryonic and fetal growth from days 20 to 100 of gestation increases from 0.06 to 1000 g. Fetal wet weight is highly correlated with placental length ($r = .64$), placental surface area ($r = .72$), and total areolae surface per placenta ($r = .65$).

Hormones during Pregnancy

Corpora lutea (CL) are essential for maintenance of pregnancy to term in the pig. Progesterone concentrations in peripheral blood increase to peak values by day 12, and gradually decrease to levels of 20 to 25 ng/ml by day 104 (Fig. 3).

Prolactin is luteotropic in the pig. Prolactin plasma levels increase markedly in late pregnancy and remain high during early lactation (Fig. 3).

Relaxin is produced and accumulated in electron dense cytoplasmic granules of porcine CL, but their concentrations in peripheral blood remain consistently low (~ 2 ng/ml) during the first 90 days, then increase to peak values 2 days before parturition and signal the discharge of accumulated relaxin from the CL (Fig. 3). A programmed peak release of relaxin occurs at day 113, and progesterone decreases by half in unmated hysterectomized gilts, events that mimic hormone changes seen in late pregnancy and parturition (Fig. 3). Relaxin and estrogen are required for remodeling collagen

and dilation of the cervix and for the growth of mammary parenchymal tissue, cervix, and vagina of late pregnant gilts.

Lactation

With the exception of the postpartum estrus, sows rarely exhibit estrus during lactation. Ovarian morphology during this anestrus period indicates an absence of gonadotropic stimulation. The average diameter of the ovarian follicle decreases (i.e., from 4 to 2 mm) during the first week after parturition and then gradually increases (i.e., more than 5 mm) by the fifth week of lactation.

Sow at Weaning

Removal of the litter from the sow after 3 to 5 weeks of lactation results in follicular development, estrus, and ovulation within 4 to 8 days. Sows can be bred at this fertile heat. At weaning, a transient increase occurs in plasma LH and hypothalamic GnRH content. During the postweaning period, plasma concentrations of estradiol-17 β increase gradually and are terminated by the preovulatory surge of LH at estrus.

TABLE 1. **Gonadal Development of Porcine Embryos.**

DAYS	M _{ale}	F _{emale}
21	Gonadal primordium	Gonadal primordium
22-24	Primitive cord cells	Primitive cord cells
	Primordial germ cells	Primordial germ cells
26	Surface epithelium	Surface epithelium
	Mesenchyme	Mesenchyme
	Testicular cords	Gonadal blastema
	Interstitial	
	Testosterone production	
27	Sertoli cells	
29	AMH production	
30-35	Leydig cells, 3 β -HSD production	Egg nests
40		Meiosis of germ cells
60	Testicular descent	Primordial follicles
70		Primary follicles
90	Testes in scrotum	Secondary follicles

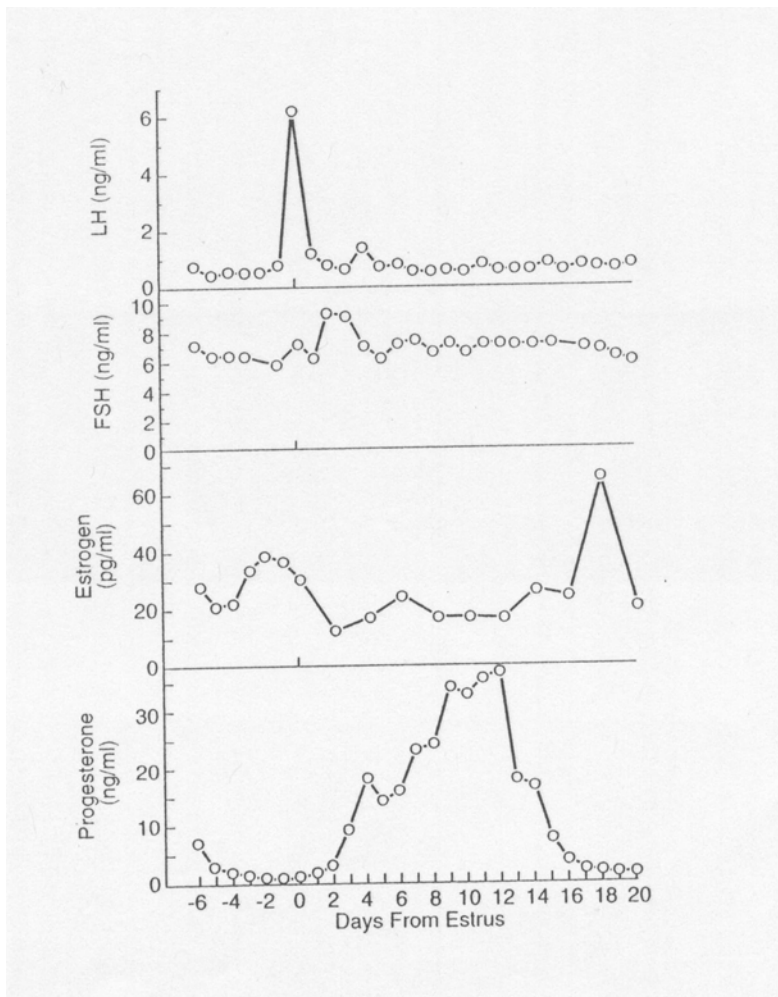


Figure 1. Peripheral blood plasma concentrations of progesterone, estrogen, FSH, and LH during the estrous cycle in the pig.

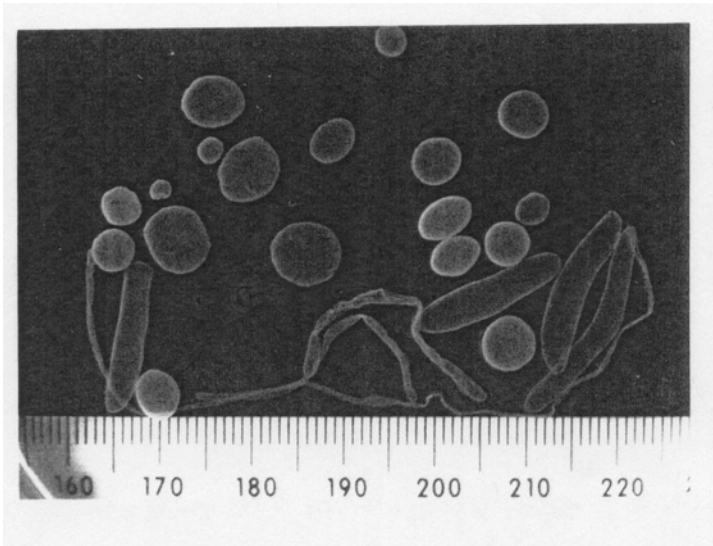


Figure 2. Picture of the diverse morphologies of pig embryos found on days 11 to 12 of gestation, including spherical, ovoid, tubular, and filamentous forms. The filamentous form can reach lengths of approximately 100 μ m. (Photomicrograph courtesy of Stephen P. Ford and Matthew E. Wilson, Iowa State University, Ames.)

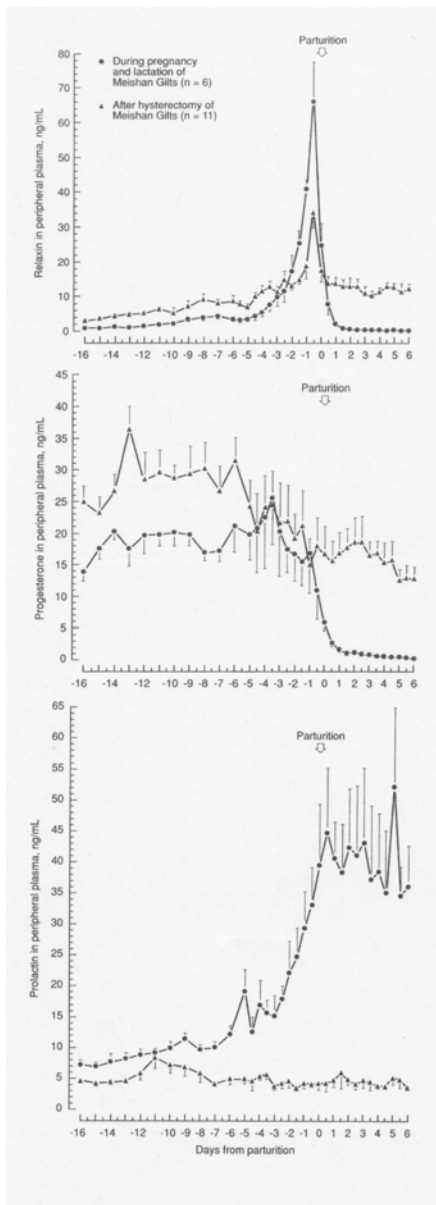


Figure 3. Relaxin, progesterone, and prolactin concentrations in peripheral plasma of Meishan gilts during pregnancy and lactation compared with those in unmated gilts hysterectomized on days 6 to 8 after estrus. Values are mean \pm SE.